ZooKeys 1270: 157–179 (2026)
DOI: 10.3897/zookeys.1270.170907

Research Article

Supplementary description and molecular analysis of *Stiphodon hadiatyae* (Teleostei, Gobioidei, Sicydiinae) from Enggano Island, Indonesia

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Abstract

The present study provides a supplementary morphological description, the first molecular analysis, and the first description of female of *Stiphodon hadiatyae* Nurjirana, Gustiano, Haryono & Wibowo, 2025. In addition, the first distributional record of the species from outside Enggano Island is noted, based on underwater photographs from Padang, Sumatra, Indonesia. Although recently described, the original account lacked both molecular data and female diagnostic characters. Phylogenetic and morphological evidence confirms placement within the "*Stiphodon sapphirinus* group" characterized by generally having 14 pectoral fin rays and a smaller adult body size (usually < 40 mm SL). *Stiphodon hadiatyae* differs from its congeners by the following characteristics: males possess a pointed first dorsal fin, with an elongated, filamentous fourth spine, fewer premaxillary tricuspid teeth, a belly entirely covered by cycloid scales, and a slightly pointed caudal fin. Coloration also distinguishes both sexes from congeners: males with a blue head with a brown snout, body greyish, median fins orange, and a distinct black blotch at caudal fin base; females with orange to red first, second dorsal, and anal fins, and a caudal fin proximally red to orange with four or five rows of brown spots.

Key words: Amphidromous, Indian Ocean, Oxudercidae, Sumatra, taxonomy

OPEN ACCESS

Academic editor: Tihomir Stefanov
Received: 22 September 2025
Accepted: 21 January 2026
Published: 23 February 2026

ZooBank: https://zoobank.org/8D07C556-ED2B-45E6-AD29-AEF33C271EEF

Citation: Jhuang W-C, Kusuma AB, Liao T-Y (2026) Supplementary description and molecular analysis of *Stiphodon hadiatyae* (Teleostei, Gobioidei, Sicydiinae) from Enggano Island, Indonesia. ZooKeys 1270: 157–179. https://doi.org/10.3897/zookeys.1270.170907

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Introduction

The genus *Stiphodon* Weber, 1895 comprises amphidromous gobies that inhabit tropical and subtropical freshwater streams from the eastern Indian Ocean to the central Pacific Ocean (Watson 1995; Maeda et al. 2015). These species exhibit a unique life history where larvae drift into marine environments before returning to freshwater to grow and reproduce (Keith et al. 2015a). Currently, 34 species of *Stiphodon* are considered valid, though taxonomic ambiguities persist for several species (Maeda 2013; Jhuang et al. 2024; Nurjirana et al. 2025). Furthermore, the genus *Stiphodon* is divided into two distinct clades: the "*Stiphodon elegans* group" sensu Keith et al. (2011), characterized by 14–16

pectoral-fin rays and a relatively larger body size (typically 4–7 cm SL), and the "*Stiphodon sapphirinus* group" sensu Keith et al. (2011), with 13 or 14 pectoral-fin rays and a smaller body size (usually < 40 mm SL) (Watson and Kottelat 1995; Keith et al. 2011; Jhuang et al. 2024).

Stiphodon exhibits high diversity in Indonesia, with 13 species documented to date, including *Stiphodon annieae* Keith & Hadiaty, 2015, *S. atropurpureus* (Herre, 1927), *S. aureofuscus* Keith, Busson, Sauri, Hubert & Hadiaty, 2015, *S. carisa* Watson, 2008, *S. hadiatyae* Nurjirana, Gustiano, Haryono & Wibowo, 2025, *S. maculidorsalis* Maeda & Tan, 2013, *S. multisquamus* Wu & Ni, 1986, *S. ornatus* Meinken, 1974, *S. pelewensis* Herre, 1936, *S. rutilaureus* Watson, 1996, *S. semoni* Weber, 1895, *S. surrufus* Watson & Kottelat, 1995, and *S. zebrinus* Watson, Allen & Kottelat, 1998 (Watson et al. 1998; Watson 2008; Maeda and Tan 2013; Keith and Hadiaty 2015; Keith et al. 2015a, 2015b; Hoese et al. 2024). Five of these species, *S. atropurpureus*, *S. carisa*, *S. maculidorsalis*, *S. ornatus*, and *S. semoni*, have been recorded in Sumatra, the largest island in western Indonesia (Watson 2008; Maeda and Tan 2013; Keith et al. 2015a).

Enggano Island, a small island off the west coast of Sumatra, remains largely unexplored for its freshwater ichthyofauna despite its geographical proximity to the mainland (Hadiaty and Sauri 2017). For centuries, surveys of island's aquatic fauna were scarce until 1893, when two fish species, *Gobius modiglianii* Perugia, 1893 and *Eleotris squamifrons* Perugia, 1893, were first described (Perugia 1893). Subsequently, no further ichthyological surveys were conducted until 2015, when a freshwater survey collected fish samples from the island's rivers, comprising 28 species belonging to 11 families and three orders (Hadiaty and Sauri 2017). From these specimens, some were identified as belonging to the genus *Stiphodon* and were suspected to be a new, as yet undescribed, species (Hadiaty and Sauri 2017). Recently, this species was formally described as *Stiphodon hadiatyae* by Nurjirana et al. (2025), based on specimens from Enggano Island. However, their description lacked molecular data and did not include female morphological information. In addition, the meristic counts reported in the abstract, diagnosis, description, supplemental tables, and taxonomic key of Nurjirana et al. (2025) are inconsistent and contradictory, further indicating the need for a supplementary and clarified description.

In this study, we provide a detailed description of *S. hadiatyae* from Enggano Island, including the first molecular analysis and the first formal description of the female. We also offer additional diagnostic morphological details that support the species' recognition within the *Stiphodon sapphirinus* group, and compare it to related congeners using both morphological and genetic data. Furthermore, we document the first record of *S. hadiatyae* from the Sumatra Island, extending its distribution range.

Materials and methods

Specimen collection and preservation

Specimens were collected from the Paco River, Malakoni Village, Enggano Island, Bengkulu (Figs 1, 2) using hand nets and immediately euthanized by hypothermia, using an ice-filled cooler. A right pectoral-fin clip was cut from each specimen and stored in 95% ethanol for molecular analysis. All specimens

were photographed, and fixed in 10% formalin, and then transferred to 70% ethanol for permanent preservation to enable further morphological examination. Specimens were deposited in the Department of Oceanography, National Sun Yat-sen University, Kaohsiung, Taiwan (DOS), and the Department of Marine Sciences, Faculty of Fisheries and Marine Sciences, Papua University (UNIPA), Indonesia. The sampling location (Fig. 1) was mapped in QGIS 3.30.0 (QGIS Development Team 2025), with basemaps (https://www.naturalearthdata.com) sourced from Natural Earth (https://www.naturalearthdata.com/downloads/; accessed on 28 April 2025).

Morphological measurements and meristic counts

Morphometric measurements followed Jhuang et al. (2024), with all measurements taken point-to-point to the nearest 0.1 mm using dial calipers under a stereomicroscope. Standard length (SL) was used as the reference; all measurements are expressed as percentages of SL. Cephalic sensory pore system and tooth counts terminology follows Nakabo (2002), while sensory papillae nomenclature follows Sanzo (1911). Cephalic sensory pores and cutaneous papillae were visualized using cyanine blue staining (Saruwatari and Andrés López 1997).

DNA extraction and phylogenetic analysis

DNA was extracted from seven specimens of *Stiphodon hadiatyae*, as well as two specimens each of the congeners *S. percnopterygionus* Watson & Chen, 1998 and *S. carisa*, using the GeneMark Easy Tissue & Cell Genomic DNA Purification kit (GeneMark, Taichung, Taiwan), following the manufacturer's protocol. A 680 bp fragment of the mitochondrial cytochrome oxidase subunit I (COI) gene was amplified via polymerase chain reaction (PCR) using the primers FishF1 (5'-TCAACCAACCACAAAGACATTGGCAC-3') and FishR1 (5'-ACTTCAGGGTGACCGAAGAATCAGAA-3') (Ward et al. 2005). PCR reactions (25 µl) contained 2 µl genomic DNA, 1.2 µl of each primer, 3 µl Pro Taq 10× Buffer, 2 µl dNTPs, 0.5 µl Pro Taq Plus DNA Polymerase (Protech, Taipei, Taiwan), and 15.1 µl ultrapure water. The thermal cycling profile for COI followed Liao et al. (2021) and consisted of 94 °C for 5 min; 37 cycles of 94 °C for 60 s, 60 °C for 45 s, and 72 °C for 60 s; and a final extension at 72 °C for 10 min. PCR products were checked by agarose gel electrophoresis, purified using the SAP–Exo purification kit (Jena Bioscience, Jena, Germany), and then commercially Sanger-sequenced. Sequence alignment and manual editing were performed using MEGA version 11 (Tamura et al. 2021), and all sequences were deposited in the GenBank nucleotide repository (accession numbers: PV203600–PV203610).

To examine the phylogenetic placement of *Stiphodon hadiatyae*, we retrieved 39 COI sequences from 20 *Stiphodon* species available in GenBank (Table 1). *Sicyopterus lagocephalus* (Pallas, 1770) (1) and *Awaous ocellaris* (Broussonet, 1782) (1) sequences were used as outgroups (Table 1). A Maximum Likelihood (ML) phylogenetic tree was reconstructed using MEGA 11, based on the HKY + G model as determined by jModelTest (Darriba et al. 2012). Bootstrap support was assessed through 1,000 replications (Felsenstein 1985).

Table 1. Accession numbers, voucher numbers, and sample sites of molecular samples.

Species	Accession numbers	Voucher numbers	Sampling sites	Sources
Stiphodon hadiatyae Nurjirana, Gustiano, Haryono & Wibowo, 2025	PV203604	UNIPA-B159	Enggano	This study
	PV203606	UNIPA-B160	Enggano	This study
	PV203610	UNIPA-B161	Enggano	This study
	PV203607	DOS10029-3	Enggano	This study
	PV203608	DOS10029-4	Enggano	This study
	PV203609	DOS10029-5	Enggano	This study
	PV203605	DOS10315	Enggano	This study
S. alcedo Maeda, Mukai & Tachihara, 2012	AB613000	NSMT-P103605	Okinawa	Maeda et al. 2011
S. annieae Keith & Hadiaty, 2015	PP132749	BIF5099	Ambon	Jamonneau et al. 2024
	PP132553	BIF5292	Seram	Jamonneau et al. 2024
S. atropurpureus (Herre, 1927)	MT646831	S atr Val 01	Negros	Direct submission
	MT646832	S atr Val 02	Negros	Direct submission
S. aureofuscus Keith, Busson, Sauri, Hubert & Hadiaty, 2015	KU693160	BIF2718	Bali	Dahruddin et al. 2016
	KU693161	BIF2046	Java	Dahruddin et al. 2016
S. carisa Watson, 2008	PV203602	DOS08610-1	Sumatra	This study
	PV203603	DOS08610-2	Sumatra	This study
S. chlorestes Jhuang, Dimaquibo & Liao, 2024	OR157890	ASIZP0081725	Taiwan	Jhuang et al. 2024
	OR157892	PNM 15728	Luzon	Jhuang et al. 2024
S. elegans (Steindachner, 1879)	HQ639084	MNHN_25A	French Polynesia	Keith et al. 2011
	HQ639085	MNHN_25B	French Polynesia	Keith et al. 2011
S. imperiorientis Watson & Chen, 1998	OR157904	DOS07277	Shenzhen	Jhuang et al. 2024
	OR157905	DOS07300	Taiwan	Jhuang et al. 2024
S. hydoreibatus Watson, 1999	HQ639075	MNHN_SHF1	Samoa	Keith et al. 2011
	HQ639076	MNHN_SHF2	Futuna	Keith et al. 2011
	HQ639077	MNHN_SH	Futuna	Keith et al. 2011
S. maculidorsalis Maeda & Tan, 2013	PP132414	BIF6009	Sumatra	Jamonneau et al. 2024
	PP132394	BIF6012	Sumatra	Jamonneau et al. 2024
S. multisquamus Wu & Ni, 1986	OR157902	DOS03177-1	Hainan	Jhuang et al. 2024
	OR157903	DOS03177-2	Hainan	Jhuang et al. 2024
S. ornatus Meinken, 1974	PP132425	BIF6051	Sumatra	Jamonneau et al. 2024
	PP132439	BIF6019	Sumatra	Jamonneau et al. 2024
S. palawanensis Maeda & Palla, 2015	OR157900	DOS08769-1	Palawan	Jhuang et al. 2024
	OR157901	DOS08769-2	Palawan	Jhuang et al. 2024
S. percnopterygionus Watson & Chen, 1998	PV203600	DOS02541-1	Taiwan	This study
	PV203601	DOS02541-2	Taiwan	This study
S. pelewensis Herre, 1936	MK496967	MNHN_atra3	Vanuatu	Lord et al. 2019
	MK496968	Aqua5409	Indonesia	Lord et al. 2019
S. pulchellus (Herre, 1927)	OR157897	DOS06170-1	Palawan	Jhuang et al. 2024
	OR157898	DOS06170-2	Palawan	Jhuang et al. 2024
S. rubromaculatus Keith & Marquet, 2007	HQ639072	MNHN_SRF1	Futuna	Keith et al. 2011
S. rutilaureus Watson, 1996	HQ639073	MNHN_21	New Caledonia	Keith et al. 2011
	HQ639074	MNHN_23	Vanuatu	Keith et al. 2011
S. sapphirinus Watson, Keith & Marquet, 2005	HQ639078	MNHN_SA28A	Vanuatu	Keith et al. 2011
	HQ639079	MNHN_SA28B	Vanuatu	Keith et al. 2011
S. semoni Weber, 1895	KU693171	BIF1711	Java	Dahruddin et al. 2016
	KU693172	BIF1709	Java	Dahruddin et al. 2016
S. surrufus Watson & Kottelat, 1995	PP132588	BIF5514	Ambon	Jamonneau et al. 2024
	PP132399	BIF5509	Ambon	Jamonneau et al. 2024
S. tuivi Watson, 1995	MK496969	MNHN_tui5477	Marquesas	Lord et al. 2019
	MK496970	MNHN_tui5479	Marquesas	Lord et al. 2019
Out-groups				
Sicyopterus lagocephalus (Pallas, 1770)	MK496948	MNHN_LP8	Vanuatu	Lord et al. 2019
Awaous ocellaris (Broussonet, 1782)	KC959856	ipon_3	Luzon	Asis et al. 2013

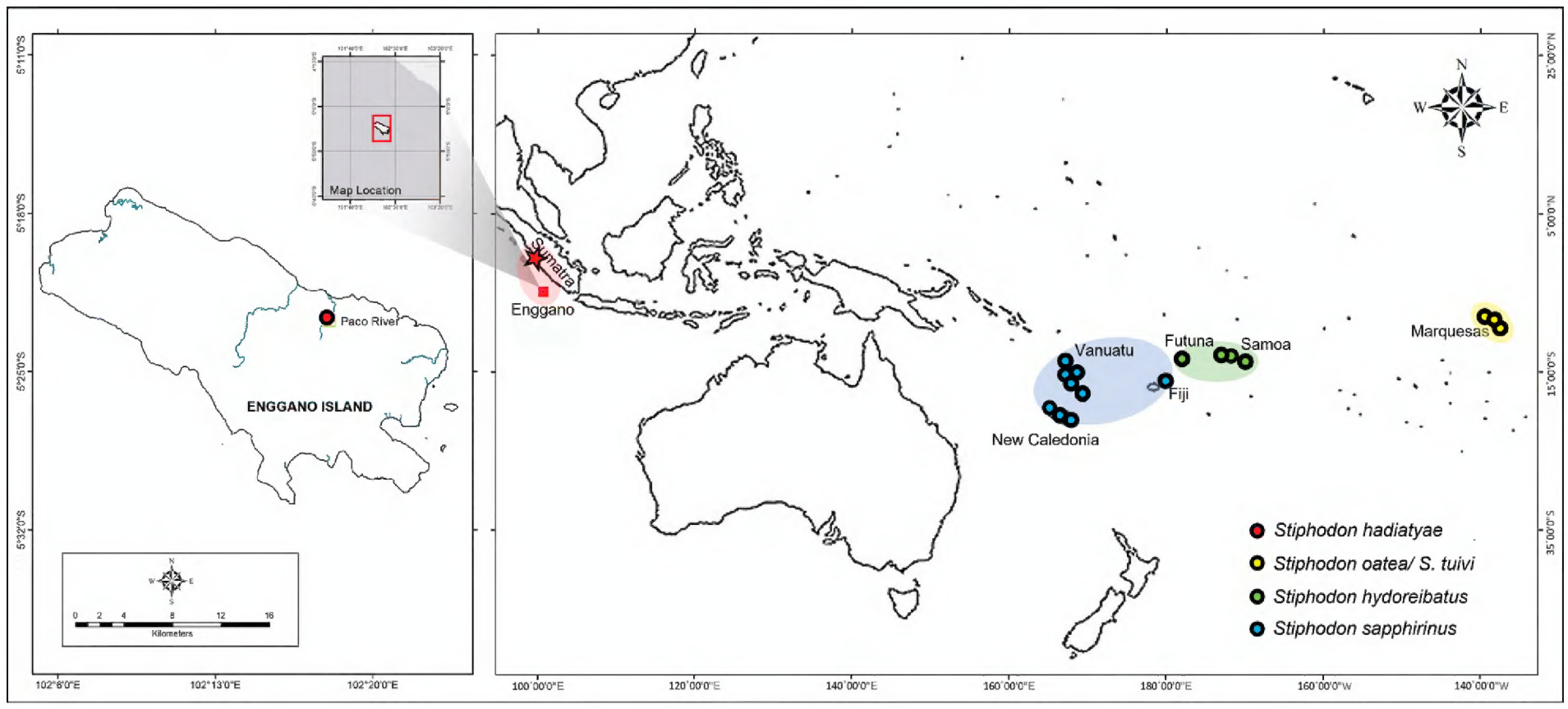

Figure 1. Map showing the recorded sites and distribution range of five closely related species of *Stiphodon*. Circles indicate the localities, with colors representing different species. A star indicates the newly recorded site of *S. hadiatyae*. The oval shaded areas indicate the distribution ranges of each species (species records based on Keith et al. 2015a; map was generated using QGIS 3.30.0).

Figure 2. Habitat of *Stiphodon hadiatyae* in the Paco River, Enggano Island, Bengkulu, southwestern Sumatra, Indonesia (photographed by WCJ).

Results

***Stiphodon hadiatyae* Nurjirana, Gustiano, Haryono & Wibowo, 2025**
Fig. 3
Common name: Renny's stiphodon goby

Material examined. Seven specimens (four males and three females, 20.8–36.3 mm SL). INDONESIA: • UNIPA-B159 (male, 27.9 mm SL) • UNIPA-B160 (male, 20.8 mm SL) • UNIPA-B161 (female, 34.2 mm SL) • DOS10029-3 (female, 26.8 mm SL)

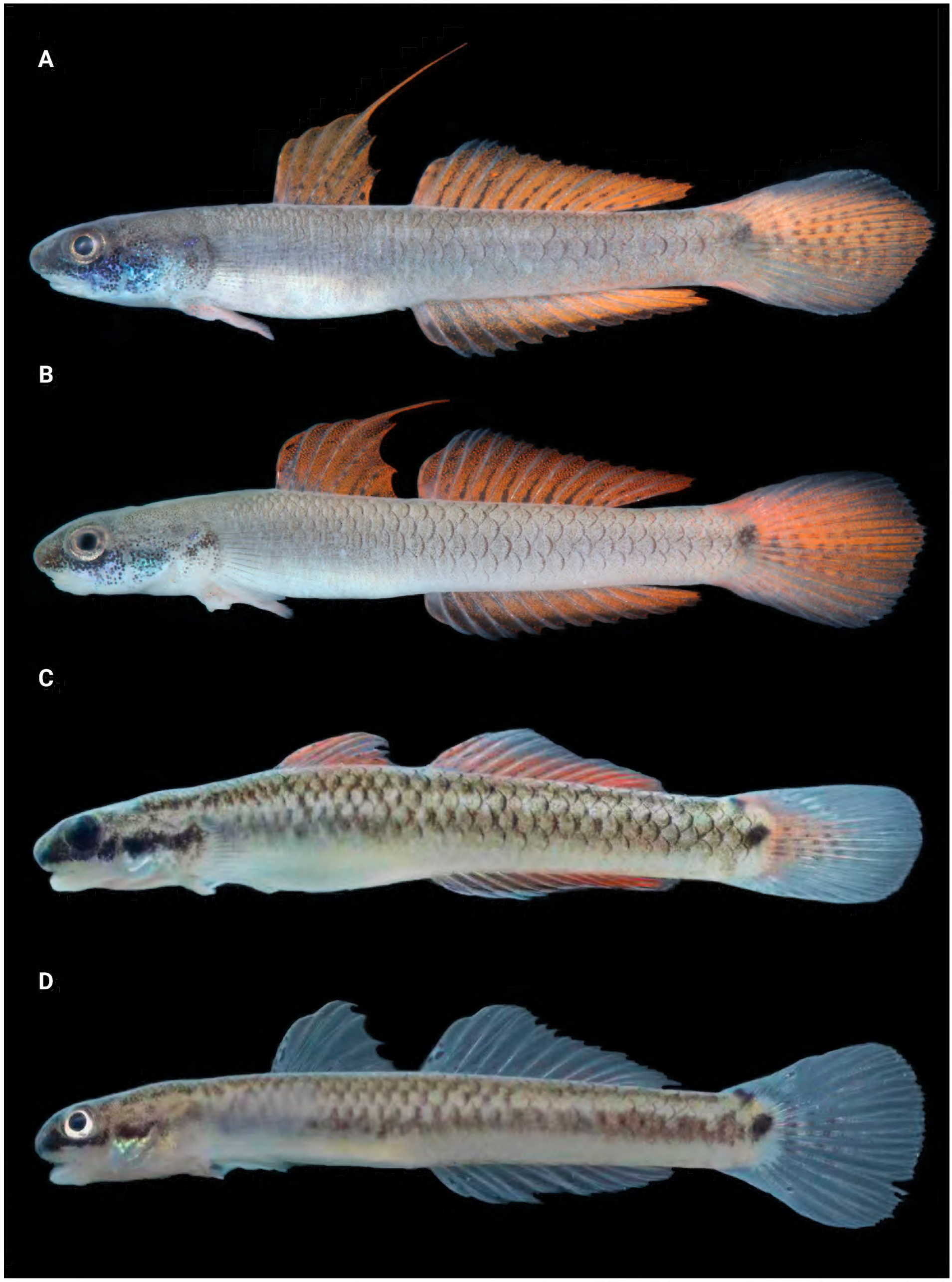

Figure 3. *Stiphodon hadiatyae*, photographed immediately after fixation. **A.** UNIPA-B159, male, 27.9 mm SL; **B.** DOS10315, male, 27.7 mm SL; **C.** DOS10029-5, female, 36.3 mm SL; **D.** DOS10029-3, female, 26.8 mm SL (photographed by WCJ).

• DOS10029-4 (male, 26.9 mm SL) • DOS10029-5 (female, 36.3 mm SL) • DOS10315 (male, 27.7 mm SL); Paco River, Malakoni Village, Enggano Island, Bengkulu, Southwestern Sumatra; 05°22'35.2S, 102°18'11.1E; coll. WCJ & ABK; 27 April 2025.

Diagnosis. *Stiphodon hadiatyae* belongs to the *Stiphodon sapphirinus* group, diagnosed by a small body size (max size < 40 mm) and usually 14 pectoral fin rays. It can be distinguished from congeners of the *Stiphodon sapphirinus* group by the following character combinations: first dorsal fin pointed with elongated and filamentous fourth spine, and a slightly pointed caudal fin in males; second dorsal fin rays 10; fewer premaxillary tricuspid teeth (21–29 in males; 21–31 in females); a belly entirely covered by cycloid scales. Coloration of males: head cobalt-blue with a brown snout; body greyish; median fins orange; distinct black blotch at caudal fin base; in females, first-, second-dorsal and anal fins orange to red; caudal fin proximally red to orange with four or five rows of brown spots.

Description. Morphometric measurements and meristic counts are given in Tables 2–8. Body slender, cylindrical anteriorly, gradually becoming compressed posteriorly; dorsal and ventral body profiles nearly straight. Head small (20.5–25.5% SL), approximately one-fifth to one-fourth of standard length. Snout short (3.7–6.4% SL) and rounded, extending slightly beyond upper jaw, and upper jaw extending beyond lower jaw. Mouth inferior; upper lip thick and smooth, with a small medial cleft. Eyes large (5.6–6.8% SL), positioned dorsolaterally. Interorbital width approximately equal to eye diameter (3.7–6.1% SL). Anterior nostril short, tubular; posterior nostril without tubular structure.

Dorsal fins VI and I, 10; in females, first dorsal fin semicircular, with the third or fourth spine longest; in males, first dorsal fin longer than female (22.1–33.0% vs 16.4–19.0% SL), with the fourth spine filamentous; in females, second ray of second dorsal fin longest; in males, second dorsal fin proportionally longer than female (34.1–40.0% vs 32.1–37.7% SL), with last ray longest. Anal fin I, 10, origin beneath origin of second dorsal fin; second ray longest in females; last ray longest in males. Pectoral fin with 14 (6) or 15 (1) rays, usually longer in males (longest ray 20.1–22.3% SL vs 19.0–21.6% SL in females; Table 2). Pelvic fins I, 5, origin directly below pectoral fin base, fused into a cup-like structure, supported by a folded fleshy frenulum. Caudal fin composed of 17 soft rays, including 13 principal caudal-fin rays; posterior margin slightly pointed in males, rounded or slightly truncated in females. Caudal fin longer in males (24.9–28.3% SL vs 20.9–25.7% SL in females; Table 2). Premaxillary teeth 21–31, fine and tricuspid (Table 3). Dentary with 1 (n = 1), 2 (n = 1), or 3 (n = 2) symphyseal teeth in males and 2 (n = 3) in females, curved and resembling canine-like shapes; dentary also with a single row of 24–34 unicuspid horizontal teeth enclosed in a fleshy sheath. Vertebral count 10 precaudal +16 caudal vertebrae (including terminal centrum) (n = 7).

Scales in longitudinal row 30–39 (Table 4). Scales in transverse series divided into two regions, back 8 (n = 3) or 9 (n = 4) (Table 5); forward 10 (n = 2), 11 (n = 3), or 13 (n = 2) (Table 6). Scales in zigzag series 7 (n = 1), 8 (n = 5) or 9 (n = 1). Predorsal scales in midline 13 (n = 3) in females, and 1 (n = 1), 11 (n = 2), or 13 (n = 1) in males (Table 7 and Fig. 4). Ctenoid scales cover most of tail and lateral sides of body. Cycloid scales distributed on dorsum of head, first and second dorsal fin base, anterior trunk, belly, anal fin base, and caudal fin base. Pectoral-fin base, cheek, and operculum naked.

Table 2. Morphometric measurements and meristic counts of *Stiphodon hadiatyae*.

	Holotype*	Paratype*	This study	
Sex	Male	Males (7)	Male (4)	Female (3)
Standard length (mm)	32.2	27.9–34.1	20.8–27.7	26.8–36.3
Morphometric characters (in % of SL)				
Head length	22.8	19.7–23.2	20.8–25.5	20.5–21.2
Snout length	3.8	3.4–4.6	5.9–6.3	3.7–6.4
Eye diameter	6.9	5.8–7.1	5.6–6.8	5.3–6.3
Postorbital length of head	10.4	6.7–11.2	9.0–12.0	8.8–9.6
Upper-jaw length	7.0	7.0–8.8	6.7–9.6	6.1–8.2
Body depth at P2 origin	14.7	13.1–15.2	11.5–13.3	11.1–12.3
Body depth at A origin	16.4	15.7–17.3	12.5–13.3	11.7–14.9
Depth of caudal peduncle	11.5	10.9–12.5	9.4–11.1	10.8–11.2
Length of caudal peduncle from A base	16.6	11.7–15.4	16.8–21.5	20.4–22.8
Length of caudal peduncle from D2 base	–	–	20.9–24.2	20.9–23.5
Predorsal length	34.8	33.9–36.0	33.0–36.5	34.4–35.1
Length of D1 base	14.2	10.5–14.5	13.5–18.1	14.6–19.0
Length of D1	36.5	26.2–45.7	22.1–33.0	16.4–19.0
Length of longest spine of D1	29.5	24.7–37.5	18.3–28.7	13.5–16.8
Interval between D1 and D2 bases	3.5	5.6–9.4	2.5–6.1	4.4–10.1
Length of D2 base	29.2	25.5–31.0	25.0–26.5	22.8–25.4
Length of D2	42.4	37.9–44.6	34.1–40.1	32.1–37.7
Length of longest ray of D2	14.8	10.5–17.4	14.1–16.5	15.2–16.0
Preanal fin length	53.9	48.6–55.1	33.8–53.1	52.9–55.8
Length of A base	32.6	27.4–32.0	25.3–28.4	23.1–25.7
Length of A	42.2	43.5–46.7	37.0–49.9	32.5–35.1
Length of longest ray of A	17.2	10.4–19.0	10.6–16.1	10.5–12.7
Length between anus to A base	3.6	2.5–4.2	3.2–3.7	3.5–4.9
Length of longest ray of P1	27.6	21.1–26.0	20.1–22.3	19.0–21.6
Length of C	30.3	30.3–34.0	24.9–28.3	23.1–25.7
Length of P2	–	–	13.8–16.1	14.0–14.9
Interorbital width	–	–	4.8–5.9	3.7–6.1
Meristic counts				
Dorsal fin rays	VI–I, 9		VI–I, 10	VI–I, 10
Anal fin rays	I, 10		I, 10	I, 10
Pectoral fin rays	14–15		14–15	14
Pelvic fin rays	I, 5		I, 5	I, 5
Caudal fin (branched rays)	13–16		13	13
Caudal fin (segmented rays)	–		17	17
Premaxillary teeth	24–36		21–29	21–31
Dentary horizontal teeth	–		24–31	29–34
Dentary symphyseal teeth	2–5		1–3	2
Scales in longitudinal row	22–31		30–33	31–39
Scales in transverse back series	7–8		8–9	8–9
Scales in transverse forward series	5–7		11–13	10–11
Scales in predorsal midline	6–10		1–13	13
Zigzag series	7–8		7–8	8–9

Abbreviations: D1 = first dorsal fin; D2 = second dorsal fin; A = anal fin; P1 = pectoral fin; P2 = pelvic fin; C = caudal fin. * Type specimens of *Stiphodon hadiatyae*, data from Nurjirana et al. (2025).

Cephalic sensory pores small, comprising A', B, C, D, F, H', K', L', N', and O'. Pore D singular, while others paired (Fig. 5). Pore A' positioned at snout tip, slightly above anterior nostril; Pore B positioned laterally near posterior nostril. Pores

Table 3. Premaxillary teeth in *Stiphodon hadiatyae* and related species.

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
S. hadiatyae	2	–	–	1	–	–	–	1	1	1	1																							
S. astilbos[1]							1	–	–	1	1	1	–	1	1																			
S. birdsong[1]								1	–	2	6	8	10	14	8	3	7	2	1	3	–	–	1	–	1									
S. discotorquatus[2]								1	–	–	–	2	1																					
S. hydoreibatus[3]															2	–	2	1	3	3	1	1	1	–	1	2	–	–	–	1	–	1		
S. julieni[4]													1	1	2	2	1	1																
S. mele[1]																1	1	1	1	1	1													
S. oatea[5]																				2	–	1	–	1										
S. percnopterygionus													1	–	–	1	–	–	–	–	1	–	–	1	–	–	–	–	1					
S. rubromaculatus[1]							1	2	2	1	–	1																						
S. rutilaureus																				1	1	–	3	–	1	2	3	–	–	3	1	1		
S. sapphirinus[3]											1	3	5	1	3	–	4	5	7	1	3	2	1	2	–	–	1	1	1	–	1			
S. surrufus					1	1	1	–	–	–	–	1	–	2	–	1																		
S. tuivi[4]														2	–	1	6	1	12	7	14	7	11	6	6	7	4	4	2	2	–	1	1	
S. zebrinus[6]																											1	–	1	–	–	–	–	1

[1] from Keith et al. (2009); [2] from Watson (1995); [3] from Watson et al. (2005); [4] from Keith et al. (2002); [5] from Keith et al. (2010); [6] from Watson et al. (1998).

Table 4. Longitudinal scales in *Stiphodon hadiatyae* and related species.

	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
S. hadiatyae																			1	1	1	2	1	–	–	–	–	1
S. astilbos[1]																	2	–	1	–	1	2	1					
S. birdsong[1]	1	–	2	6	3	7	5	8	6	5	4	2	4	2	–	2	2	2	–	1	1	1						
S. discotorquatus[2]																	1	–	1	–	1	–	1					
S. hydoreibatus[3]												1	–	–	2	2	1	2	2	2	3	1	–	1				
S. julieni[4]																				1	1	2	2	1	1			
S. mele[1]			2	–	–	1	1	–	1	2																		
S. oatea[5]																						1	2	–	–	–	1	1
S. percnopterygionus																					2	–	–	1	–	–	–	2
S. rubromaculatus[1]					1	1	2	1	–	2																		
S. rutilaureus																				2	4	3	5	1	1			
S. sapphirinus[3]										1	1	2	2	4	5	5	9	3	3	3	2	1	1	1				
S. surrufus								1	–	–	1	–	–	1	1	–	–	–	–	1	1	–	–	–	1			
S. tuivi[4]												1	6	5	3	8	6	9	11	7	6	8	4	7	3	2	1	1
S. zebrinus[6]																					3							

[1] from Keith et al. (2009); [2] from Watson (1995); [3] from Watson et al. (2005); [4] from Keith et al. (2002); [5] from Keith et al. (2010); [6] from Watson et al. (1998).

Table 5. Transverse back scales in *Stiphodon hadiatyae* and related species.

	2	3	4	5	6	7	8	9	10	11	12	13	14	15
S. hadiatyae							3	4						
S. astilbos[1]								7						
S. birdsong[1]	1	–	–	1	–	–	4	3	3	14	16	14	7	1
S. discotorquatus[2]									4					
S. hydoreibatus[3]								3	13					
S. julieni[4]							4	4						
S. mele[1]		1	1	3	2	1								
S. oatea[5]									3	2				
S. percnopterygionus							1	4						
S. rubromaculatus[1]						2	4	1						
S. rutilaureus									10	6				
S. sapphirinus[3]									40	1	1			
S. surrufus									2	–	2	2	1	
S. tuivi[4]									7	43	26	7	1	
S. zebrinus[6]										3				

[1] from Keith et al. (2009); [2] from Watson (1995); [3] from Watson et al. (2005); [4] from Keith et al. (2002); [5] from Keith et al. (2010); [6] from Watson et al. (1998).

C and D between eyes. Oculoscapular canal divided into anterior and posterior segments between pores H' and K'. Cutaneous sensory papillae well-developed on head (Fig. 5). Infraorbital papillae short, in six transverse rows. Row *c* between nostril and upper lip, forming transverse and longitudinal papillae. Row *d* above posterior mouth edge. Rows *e* and *i* adjacent. Row *f* at tip of jaw. Rows *g*, *m*, and *o* on dorsum of head. Rows *ot*, *oi*, and *os* well-separated on preopercle. Row *s* anterior to anterior nostril. Row u^1 above pores F and H'. Row u^2 and *x* above pores H', and K'. Row *y* above pore L'. Row *z* below pore H' (Fig. 5). Urogenital papilla conical in males with a pointed posterior edge, and broader and rounded in females.

***Color in preservation*.** Sexual dichromatism well developed. In males, dorsal and side of body dark grey, ventral white; dorsum of head dark; occipital region to nape light grey. Pectoral fin base black; pectoral fin membranes translucent. First dorsal-, second dorsal- and anal-fin spines and rays white with black spots. First dorsal-

Table 6. Transverse forward scales in *Stiphodon hadiatyae* and related species.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15		16	17	18	19	20
S. hadiatyae											2	3	–	2								
S. astilbos[1]											2	3	3	3	4							
S. birdsong[1]	2	–	2	6	2	7	7	13	9	5	4	4	1	1	–	–		–	–	1		
S. discotorquatus[2]										1	1	–	1									
S. hydoreibatus[3]											2	3	3	3	4							
S. julieni[4]										2	2	3	1									
S. mele[1]	3	2	–	–	–	–	1	1														
S. oatea[5]														1	1	2		1				
S. percnopterygionus									1	1	1	2										
S. rubromaculatus[1]		2	2	1	2																	
S. rutilaureus										2	4	4	6									
S. sapphirinus[3]								2	3	6	7	8	6	5	3	2						
S. surrufus	1	–	–	–	1	–	–	–	–	3	–	–	2									
S. tuivi[4]													2	8	7	29		20	18	4	1	
S. zebrinus[6]														1	1	1						

[1] from Keith et al. (2009); [2] from Watson (1995); [3] from Watson et al. (2005); [4] from Keith et al. (2002); [5] from Keith et al. (2010); [6] from Watson et al. (1998).

Table 7. Predorsal scales in *Stiphodon hadiatyae* and related species.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
S. hadiatyae M	–	1	–	–	–	–	–	–	–	–	–	2	–	1				
S. hadiatyae F														3				
S. astilbos M[1]				1	–	–	–	1	–	–	1	1						
S. astilbos F[1]				1	–	–	–	–	–	1	–	–	1					
S. birdsong M[1]	32																	
S. birdsong F[1]		55																
S. discotorquatus M[2]			2															
S. discotorquatus F[2]									1	–	1							
S. hydoreibatus M[3]		5	–	–	1													
S. hydoreibatus F[3]			2	–	–	3	–	–	1	–	2	2	2	2	1			
S. julieni M[4]											2	–	1	1	1			
S. julieni F[4]														2	1			
S. mele M[1]	5																	
S. mele F[1]	1	1																
S. oatea M[5]													1	1				
S. oatea F[5]															1	1	–	1
S. percnopterygionus M												1			1			
S. percnopterygionus F															2	–	1	
S. rubromaculatus M[1]		6																
S. rubromaculatus F[1]		1																
S. rutilaureus M								2	4	5	4	1						
S. sapphirinus M[3]	27	–	1	–	–	–	1											
S. sapphirinus F[3]	3	–	–	1	–	–	1	3	2	–	1	1	1					
S. surrufus M	3																	
S. surrufus F		2	–	1														
S. tuivi M[4]	10	6	7	8	6	2	7	6	7	4	5	1	–	2	1			
S. tuivi F[4]		1	–	–	–	–	4	2	2	2	5	5	2	3	1			
S. zebrinus M[6]										1								
S. zebrinus F[6]								1	–	–	–	–	–	–	1			

[1] from Keith et al. (2009); [2] from Watson (1995); [3] from Watson et al. (2005); [4] from Keith et al. (2002); [5] from Keith et al. (2010); [6] from Watson et al. (1998).

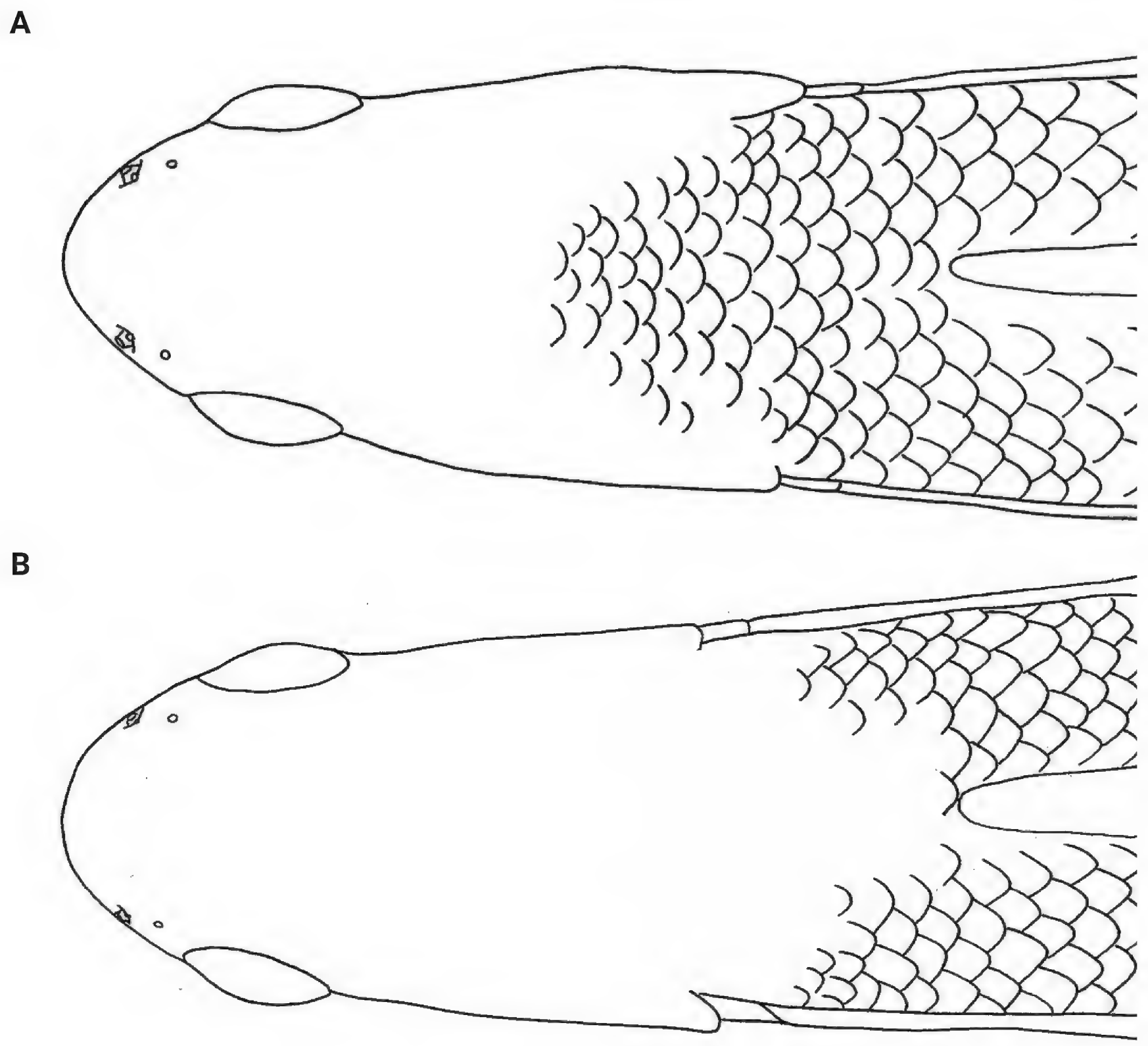

Figure 4. Predorsal squamation of *Stiphodon hadiatyae*. **A.** UNIPA-B159, male, 27.9 mm SL; **B.** DOS10315, male, 27.7 mm SL; **C.** DOS10029-5, female, 36.3 mm SL (Drawings by WCJ).

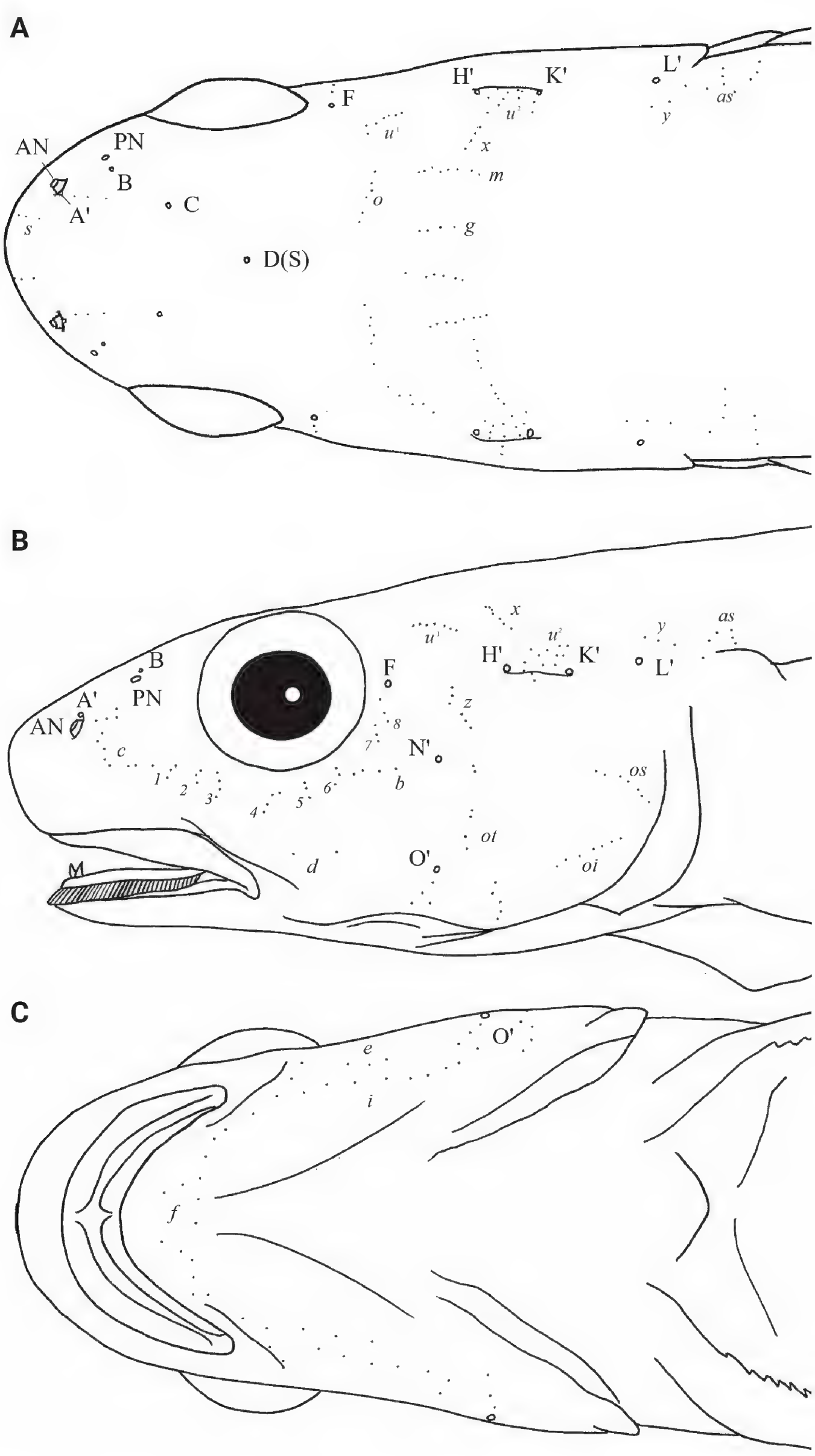

Figure 5. Diagrammatic illustration of head showing arrangement of the cephalic sensory pores and cutaneous sensory papillae in *Stiphodon hadiatyae*. (UNIPA-B159, male, 27.9 mm SL). **A.** Dorsal view; **B.** Lateral view; **C.** Ventral view. Abbreviations: AN = anterior nostril; PN = posterior nostril; A', B', C, D (S for singular), F, H' = pores of the anterior oculoscapular canal; K' and L' = pores of the posterior oculoscapular canal; N' and O' = pores of the preopercular canal. *as*, *b*, *c*, *d*, *e*, *f*, *g*, *l*, *m*, *o*, *oi*, *ot*, *os*, *s*, *u*, *x*, *y*, and *z* = rows of cutaneous sensory papillae; rows 1–8 = infraorbital papillae (Drawings by WCJ).

and second dorsal-fin membrane light red. Anal fin light red, distal margin black. Caudal fin light red with pale-white and black spots with 8–10 transverse bars on middle of fin; a black blotch at caudal fin base. Pelvic fin rays and frenulum white; fin membrane transparent; fin rays and fin membrane with melanocytes, mainly on distal margin. In females, background of body and head cream; two black longitudinal bands extending through body and forming black blotches at end, one extending from upper lip to end of caudal peduncle through lateral midline; another extending from snout through eye to upper edge of caudal peduncle. Dorsum dusky; first and second dorsal-fin membranes almost red or transparent; usually two or three black spots along each spine and rays. Anal fin membrane transparent; black sub-margin distally; one or two black spots along each spine and rays. Caudal fin transparent with four or five transverse bands composed of black spots on middle of fin. Pectoral-fin membranes translucent. Pelvic fin translucent, usually with dense melanocyte at base and middle of rays, membranes, and frenulum.

***Color in life*.** Body and fin markings of male and female similar to those of preserved specimens. Males usually silver-grey in background of body; head grey or brown; ventral part of head to belly white; eyes cream color. First and second dorsal fins red to orange, fin-rays with 3–5 rows of black and white spots, membranes with a vertical brown stripe or 3–5 brown spots; pectoral fins transparent; anal fin white to light red with a broad black band along distal margin; caudal fin red to orange, fin-rays with 7–9 rows of brown spots, upper fin edge transparent (Figs 3a, b, 6a, b). In nuptial coloration, male's cheeks metallic blue or metallic green. Females usually pale yellowish-brown in background of body and head; eyes cream color; first dorsal, second dorsal, and anal fins orange to red (small size transparent); pectoral fins transparent; caudal fin rays with four or five rows of brown spots, proximal red to orange, distal transparent; body markings similar to preserved specimens (Figs 3c, d, 6c).

Distribution and habitat. *Stiphodon hadiatyae* was previously known only from its type locality, the Paco River in Malakoni Village, Enggano Island, Bengkulu, Southwestern Sumatra, Indonesia (Fig. 1). This study provides the first record of the species from outside Enggano Island, based on recent underwater photographs taken by aquarium hobbyists in the Pisang River in Padang, Sumatra (Fig. 6d). The habitat substrate consists of gravel and sand (Fig. 2). In Enggano Island, it was found together with two other sicydiine goby species, *Lentipes niasensis* Harefa & Chen, 2022 and *Sicyopterus micrurus* (Bleeker, 1854).

Molecular analysis. A total of 52 sequences (680 bp) from 25 species were analysed to reconstruct a Maximum Likelihood (ML) phylogenetic tree (Fig. 7) rooted with the outgroup taxa *Awaous ocellaris* and *Sicyopterus lagocephalus*. The tree topology revealed that sequences of *Stiphodon hadiatyae* form a monophyletic clade. Phylogenetically, *S. hadiatyae* is sister to a clade comprising *S. hydoreibatus*, *S. sapphirinus*, and *S. tuivi*. Together, these four species form a clade that is sister to another clade containing *S. rubromaculatus*, *S. surrufus*, and *S. rutilaureus*. The genetic distances between *S. hadiatyae* and other members of the *S. sapphirinus* group range from 9.4% to 11%. (Table 8).

Remarks. The morphological description and meristic counts of *Stiphodon hadiatyae* in the present study are generally consistent with those reported by Nurjirana et al. (2025), but several differences are noted. These include the belly being fully covered with scales (vs always without scales in Nurjirana et al. (2025)); more second dorsal-fin rays (10 vs 9); longer snout length in males (5.9–6.3% vs 3.4–

Figure 6. Live coloration of *Stiphodon hadiatyae*. **A.** Male collected from Enggano Island (DOS10315, 27.7 mm SL, aquarium photo, photographed by WC Huang); **B.** Male collected from Enggano Island (ca 35 mm SL, not preserved, aquarium trade in China, 9 Aug. 2024, photographed by WK Chen); **C.** Female collected from Enggano Island (ca 20 mm SL, not preserved, aquarium trade in China, 1 Jan. 2022, photographed by HQ Chen); **D.** Male photographed underwater (ca 40 mm SL, not preserved, newly recorded from the Pisang River, Padang, Sumatra, 25 Jun. 2025, photographed by CY Tse).

4.6% SL); smaller body depth at pelvic fin origin (11.1–13.3% vs 13.1–15.2% SL), and body depth at the anal fin origin (11.7–14.9% vs 15.7–17.3% SL). These discrepancies may be attributable to differences in measurement methods among researchers. In addition, prolonged storage of specimens (their material was collected by Renny K. Hadiaty and Sopian Sauri on 26 April 2015) or suboptimal preservation conditions may have resulted in scale loss or specimen shrinkage.

Stiphodon hadiatyae can be distinguished from five other species from Sumatra, *S. atropurpureus*, *S. carisa*, *S. maculidorsalis*, *S. ornatus*, *S. semoni*, based on a combination of morphological characters. It differs from *S. atropurpureus*, *S. carisa*, and *S. semoni* by lacking fatty tissue behind pectoral fin base in males (vs with a white attachment), presence of an elongated and filamentous first dorsal fin spine in males (vs absence), and pectoral fin rays usually 14 (vs usually 15); from *S. maculidorsalis* and *S. ornatus* by the presence of an elongated and filamentous first dorsal fin spine in males (vs not filamentous), pectoral fin rays usually 14 (vs usually 15–16), and lacking spots on pectoral fin (vs 3–8 rows of black and white spots on pectoral fin rays in both sexes) (Maeda and Tan 2013). In addition, females of *S. hadiatyae* have the first and second dorsal, anal, and caudal fins orange to red, a condition not observed in females of those five Sumatran congeners (Maeda and Tan 2013; Keith et al. 2015a).

Stiphodon hadiatyae differs from *S. alcedo*, *S. annieae*, *S. chlorestes*, *S. imperiorientis*, *S. larson*, *S. martenstyni*, *S. multisquamus*, *S. niraikanaiensis*, *S. pelewensis*, and *S. pulchellus* in having typically 14 pectoral fin rays (vs 15–16) (Watson 1996, 1998; Maeda et al. 2011; Maeda 2013); from *S. astilbos* by presence of an elongated and filamentous first dorsal fin spine (vs absence), a black blotch on caudal fin base (vs absence) in males, more scales in longitudinal row in both sexes (30–39 vs 24–29) (Ryan 1986); from *S. aureofuscus* by a greater number of scales in the transverse forward series (10–13 vs 6–8) and presence of cycloid scales on belly (vs without scales) (Keith et al. 2015b); from *S. caeruleus* by more scales in

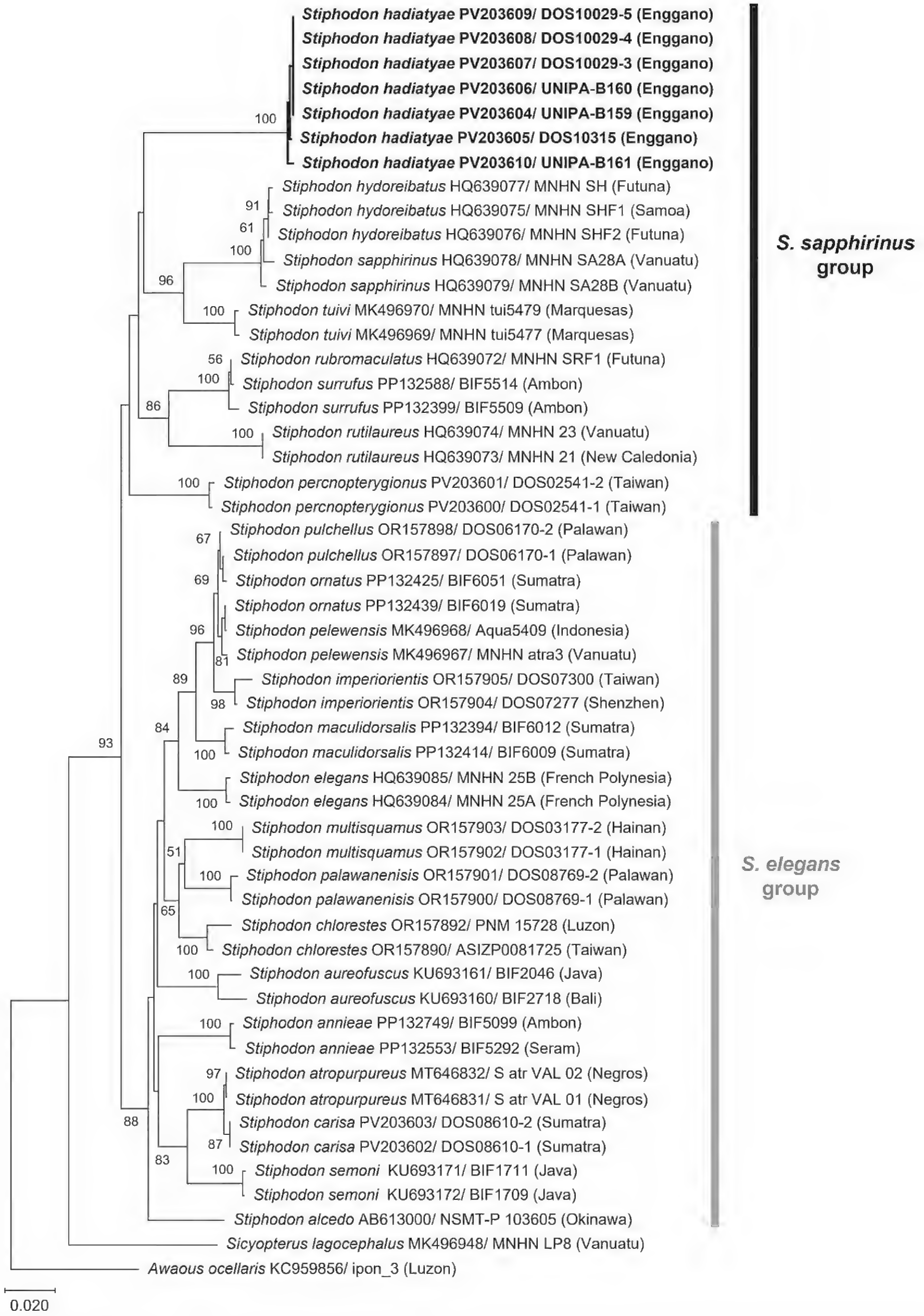

Figure 7. The Maximum Likelihood (ML) phylogenetic tree was constructed using COI sequences (680 bp) from 23 species of *Stiphodon*, along with the outgroup genera *Sicyopterus* and *Awaous*. Bootstrap values are indicated beside the internal branches, but intraspecific bootstrap values and values below 50 are not shown. Labels following the scientific names represent GenBank accession numbers, voucher numbers, with sampling sites given in brackets.

Table 8. Mean COI (680 bp) K2P genetic distances of inter- (below diagonal) and intra-species (bolded on diagonal) of the *Stiphodon sapphirinus* group.

	S. hadiatyae	*S. hydoreibatus*	*S. percnopterygionus*	*S. rubromaculatus*	*S. rutilaureus*	*S. sapphirinus*	*S. surrufus*	*S. tuivi*
	(*n* = 7)	(*n* = 3)	(*n* = 2)	(*n* = 1)	(*n* = 3)	(*n* = 2)	(*n* = 2)	(*n* = 2)
S. hadiatyae	**0.001**							
S. hydoreibatus	0.107	**0.002**						
S. percnopterygionus	0.104	0.088	**0.003**					
S. rubromaculatus	0.094	0.086	0.065	n/c				
S. rutilaureus	0.112	0.104	0.081	0.062	**0.000**			
S. sapphirinus	0.107	0.007	0.089	0.089	0.100	**0.006**		
S. surrufus	0.100	0.091	0.068	0.002	0.064	0.093	**0.005**	
S. tuivi	0.098	0.057	0.088	0.068	0.090	0.056	0.072	**0.003**

longitudinal row in both sexes (30–39 vs 18–21), presence of scales on belly (vs absence), and body silver-grey (vs blue) in males (Parenti and Maciolek 1993); from *S. discotorquatus* and *S. julieni* by absence of spots on pectoral fin rays (vs with alternating spots of black and white on each pectoral fin ray), and absence of spots on second dorsal fin rays (vs black and white spots on each second dorsal fin ray) in both sexes (Watson 1995; Keith et al. 2002); from *S. kalfatak* by lack of fatty tissue behind pectoral fin base in males (vs with a white attachment in males) and having an elongated and filamentous first dorsal fin spine (vs absence) (Keith et al. 2007); from *S. mele*, *S. rubromaculatus*, and *S. surrufus* by presence of an elongated and filamentous first dorsal fin spine in males (vs absence), scales on belly (vs absence), more scales in longitudinal row (30–39 vs < 30), more scales in transverse forward series (10–13 vs < 10) in both sexes, and body silver-grey in males (vs orange to red in males) (Keith and Marquet 2007; Keith et al. 2009); from *S. percnopterygionus* by fewer transverse back series (8–9 vs 10–11) and premaxillary tricuspid teeth (21–31 vs 33–46) in both sexes; from *S. rutilaureus* and *S. zebrinus* by fewer transverse back series (8–9 vs > 10) and premaxillary tricuspid teeth (21–31 vs > 40) in both sexes, and by coloration (males pale; females cream with two black longitudinal bands vs dusky transverse bars on side in both sexes; Watson et al. 1998).

Stiphodon hadiatyae is morphologically similar to *S. hydoreibatus*, *S. oatea*, *S. sapphirinus*, and *S. tuivi*, as their differences in morphometric measurements and meristic counts are relatively minor (Watson 1995, 1999; Watson et al. 2005; Keith et al. 2010). However, *S. hadiatyae* can be distinguished from *S. hydoreibatus*, *S. oatea*, *S. sapphirinus*, and *S. tuivi* by fewer premaxillary tricuspid teeth (21–36 vs 35–52 in *S. hydoreibatus*, 40–44 in *S. oatea*, 31–51 in *S. sapphirinus*, and 34–53 in *S. tuivi*). Additionally, it differs from *S. oatea*, *S. sapphirinus*, and *S. tuivi* by fewer scales in the transverse back series (8–9 vs > 10). Furthermore, *S. hadiatyae* can be distinguished from all these species by differences in body coloration and distribution (Fig. 6) (Watson 1995, 1999; Watson et al. 2005; Keith et al. 2010).

Since females of the *Stiphodon sapphirinus* group are superficially similar in color pattern, a comparative diagnosis based on female characters is provided. Females of *S. hadiatyae* can be distinguished from *S. discotorquatus*, *S. julieni*, and *S. tuivi* by pectoral-fin rays without alternating black and white spots (vs present); from *S. caeruleus* by belly with scales (vs absent); from *S. astilbos*, *S. oatea*, and *S. percnopterygionus* by black spots on first and second dorsal and

proximal caudal fin rays (vs absent in those species); from *S. hydoreibatus* and *S. sapphirinus* by black spots on first dorsal fin rays (vs absent); from *S. mele*, *S. rubromaculatus*, and *S. surrufus* by more predorsal midline scales (vs absent or few) and black spots on proximal caudal fin (vs absent); from *S. rutilaureus* and *S. zebrinus* by sides without dusky transverse bars (vs present).

The ML tree based on COI genes showed that the genus *Stiphodon* is monophyletic and can be divided into two groups, consistent with the results of Keith et al. (2011), Taillebois et al. (2014), and Jhuang et al. (2024). However, relationships within the "*S. sapphirinus* group" are poorly supported, resulting in uncertainty regarding the phylogenetic positions of some species within this group, which may be attributable to incomplete taxon sampling. In addition, several *Stiphodon* species are not recovered as monophyletic, potentially due to misidentifications or the limited resolution of single-gene analyses, suggesting that additional genetic markers are needed to clarify their taxonomic status.

Based on both morphological and molecular evidence, the present study indicates that *Stiphodon hadiatyae* is sister to the clade comprising *S. hydoreibatus*, *S. sapphirinus*, and *S. tuivi*, and belongs to the "*S. sapphirinus* group" (Fig. 7). *Stiphodon hadiatyae* is distributed in western Sumatra and Enggano Island, whereas *S. tuivi* is currently known only from Marquesas, *S. hydoreibatus* from Futuna to Samoa, and *S. sapphirinus* from New Caledonia, Fiji, and Vanuatu (Fig. 1). Although phylogenetic relationships within the *S. sapphirinus* group remain weakly supported due to incomplete taxon sampling and the use of a single mitochondrial marker, the observed distribution pattern is broadly consistent with the biogeographic scenario proposed by Taillebois et al. (2014), which suggested that *Stiphodon* dispersed from the Indonesian shelf to Melanesia, followed by subsequent diversification.

Taxonomic key to distinguish *Stiphodon* in Sumatra

Abbreviations: D1 = first dorsal fin; D2 = second dorsal fin; A = anal fin; P1 = pectoral fin.

1 Males with fatty tissue behind pectoral-fin base.....**2**
– Males without fatty tissue behind pectoral-fin base.....**4**
2 D1 triangular and elongate in male ..... ***S. carisa***
– D1 rounded in male **3**
3 D1 and D2 grey with a reddish margin in males..... ***S. atropurpureus***
– D1 and D2 pale grey/transparent, without red margin in males ..... ***S. semoni***
4 P1 with 3–8 rows of alternating black and white spots in both sexes.....**5**
– P1 without spots in both sexes ..... ***S. hadiatyae***
5 Many black spots on nape and occipital region in both sexes .... ***S. maculidorsalis***
– A few black spots on nape and occipital region in both sexes..... ***S. ornatus***

Comparative material examined

***Stiphodon annieae*:** five specimens • DOS07332, 22.1–24.8 mm SL, Maluku, aquarium trade, 15, January, 2020, coll. WC Jhuang. ***Stiphodon atropurpureus*:** 20 specimens • DOS09876, 23.4–42.3 mm SL, Luzon, 23 June 2023,

coll. AC Dimaquibo, CC Yu & NS Leung. ***Stiphodon carisa*:** six specimens • DOS08610, 32.1–37.3 mm SL, Sumatra, aquarium trade, 14 March 2022, coll. WC Jhuang. ***Stiphodon chlorestes*:** one specimen • PNM 15728, holotype, 29.6 mm SL, Luzon, 12 January, 2023, coll. WC Jhuang, AC Dimaquibo, GC Liu & KH Chen; one specimen • ASIZP0081725, paratype, 30.3 mm SL, Taiwan, 15 October, 2022, coll. WC Liang; five specimens • ASIZP0081724 • DOS09263 • NMMBA-P038532–33 • PNM 15729, paratypes, 28.6–40.2 mm SL, Luzon, 12 January, 2023, coll. WC Jhuang, AC Dimaquibo, GC Liu & KH Chen. ***Stiphodon imperiorientis*:** one specimen • DOS09250, 27.7 mm SL, Taiwan, 14 March, 2023, coll. WC Jhuang; one specimen • DOS09258, 31.1 mm SL, Taiwan, 7 April, 2023, coll. W. C. Liao; one specimen • DOS09259, 39.2 mm SL, Taiwan, 9 April, 2023, coll. WC Jhuang. ***Stiphodon multisquamus*:** two specimens • DOS03177, 58.3–62.4 mm SL, Hainan, 7 September, 2020, coll. WC Jhuang; one specimen • DOS09260, 26.7 mm SL, Taiwan, 18 July, 2021, coll. MT Zhou. ***Stiphodon palawanensis*:** five specimens • DOS09268, 43.6–51.4 mm SL, Palawan, 24 April, 2023, coll. WC Jhuang, WC Huang & BA Balisco. ***Stiphodon pelewensis*:** ten specimens • DOS10737, 36.6–45.6 mm SL, Papua, 13 September, 2024, coll. WC Jhuang. ***Stiphodon pulchellus*:** two specimens • DOS09318, 51.1–55.6 mm SL, Palawan, 26 April, 2023, coll. WC Jhuang, WC Huang & BA Balisco. ***Stiphodon percnopterygionus*:** five specimens • DOS09249, 21.1–31.0 mm SL, Luzon, 12 January 2023, coll. WC Jhuang, AC Dimaquibo, GC Liu & KH Chen. ***Stiphodon rutilaureus*:** 16 specimens • DOS10740, 20.8–27.7 mm SL, Biak, aquarium trade, 20 February 2025, coll. WC Jhuang. ***Stiphodon semoni*:** six specimens • DOS10736, 28.8–33.0 mm SL, Papua, 13 September 2024, coll. WC Jhuang. ***Stiphodon surrufus*:** 11 specimens • DOS10735, 24.9–30.3 mm SL, Papua, 13 September 2024, coll. WC Jhuang.

Acknowledgements

We are grateful to the National Research and Innovation Agency (BRIN) for granting us permission to collect data on Enggano Island. We also thank Wen-Chien Huang, Wei-Kang Chen, and Han-Qun Chen for providing photographs of live specimens, Chung Yi Tse for providing underwater photographs from the wild, Kuan-Hsun Chen for his assistance with radiographing specimens, and Jen-Ying Chen for helping with morphological analysis. Additionally, we sincerely appreciate the editors and reviewers for their dedication and efforts in improving this article.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

All specimens used in this study were collected under authorization from the National Research and Innovation Agency, Indonesia (BRIN), under research permit issued to WCJ (611A/SIP/IV/FR/4/2025) and to TYL (609A/SIP/IV/FR/4/2025) for collecting samples in Bengkulu. Additionally, none of the *Stiphodon* species involved in this study are listed as protected under Indonesia's Wildlife Conservation Act.

Use of AI

No use of AI was reported.

Funding

Higher Education SPROUT Project, Taiwan.

Author contributions

WCJ and TYL designed the study. WCJ and ABK collected the specimens. WCJ identified and photographed the specimens, generated and analysed data, and prepared the manuscript. ABK, and TYL revised the manuscript. All authors read and approved the final version of the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.

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